

## **Alien invasions and livelihoods: Economic benefits of invasive Australian Red Claw crayfish in Jamaica**

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### **Ecological Economics**

DOI:

[10.1016/j.ecolecon.2015.02.012](https://doi.org/10.1016/j.ecolecon.2015.02.012)

Published: 21/02/2015

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*

Pienkowski, T., Williams, S., McLaren, K., Wilson, B., & Hockley, N. (2015). Alien invasions and livelihoods: Economic benefits of invasive Australian Red Claw crayfish in Jamaica. *Ecological Economics*, 112, 68-77. <https://doi.org/10.1016/j.ecolecon.2015.02.012>

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# Alien invasions and livelihoods: economic benefits of invasive Australian Red Claw crayfish in Jamaica

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## Abstract

1 Invasive species have caused widespread economic and  
2 environmental disruption, which have been widely  
3 studied. However, their potential benefits have received  
4 much less attention. If invasive species contribute to  
5 livelihoods, their eradication may negatively impact  
6 wellbeing. Failing to value these benefits may lead to an  
7 undervaluation of invaded ecosystems. We assess the  
8 potential economic benefits of an invasive species within  
9 an artisanal fishery in Jamaica. We monitored catches  
10 over 259 fisherman-days, and conducted 45 semi-

11 structured interviews, with 76 fishermen. We show that  
12 the invasive Australian Red Claw crayfish (*Cherax*  
13 *quadricarinatus*) is an important source of income for  
14 fishermen within the Black River Lower Morass of  
15 Jamaica and supplement incomes during periods when  
16 native shrimp (*Macrobrachium spp.*) catches decline. We  
17 also show that full-time fishermen and those who have no  
18 alternative occupations expend the greatest fishing effort.  
19 We use the intra-annual variation of fishermen's harvest  
20 effort between seasons (when catch per unit effort  
21 changes) as a proxy for dependence. Using this  
22 measure, we found that the least wealthy appear to be  
23 the most dependent on fishing, and consequently benefit  
24 the most from the invasive crayfish. Our results  
25 demonstrate the importance of considering the potential  
26 benefits of invasive species within integrated landscape  
27 management.

28 **Keywords:** Invasive alien species. Invaded ecosystems.  
29 Small-scale fishery. Ecosystem services. Wild-harvest  
30 products.

31

## 32 **1. Introduction**

33 There is strong evidence that invasive alien species (IAS)  
34 have damaged ecological and economic systems around  
35 the world (McGeoch *et al.* 2010; Pejchar & Mooney 2009;  
36 Sala *et al.* 2000). Yet, there is little research investigating  
37 the potential economic benefits of IAS (Young 2010;  
38 Pejchar & Mooney 2009). Of the few studies that have  
39 explored the economic benefits of IAS (e.g. Shackleton *et*  
40 *al.* 2006; de Neergaard *et al.* 2005; Geesing *et al.* 2004;  
41 Jakubowski *et al.* 2001) even fewer have quantified the  
42 income that they generate (Schlaepfer *et al.* 2011, but  
43 see: Shackleton, Kirby & Gambiza (2011); Pascual *et al.*  
44 2009; Ackefors 1999; Southwick & Southwick 1992). It is  
45 unclear whether this is because IAS are near-universally  
46 destructive or because of a bias within the academic  
47 community (Stromberg *et al.* 2009; Gurevitch & Padilla  
48 2004).

49

50 A lack of appreciation of the potentially positive role of  
51 some IAS in human livelihoods may lead to a number of

undesirable outcomes. First, undervaluing the benefits of IAS may lead to excessive investment in their removal. For instance, *Lantana camara* L. is a widely studied invasive shrub (van Wilgen *et al.* 2004), considered to be among the top ten worst invasive species in the world (GISIN 2012). The majority of studies conducted to determine the economic and ecological costs and benefits of removal have not quantified the positive role this species can play as a harvestable resource for communities, such as a source of firewood or craft materials (e.g. Marais & Wannenburgh 2008; Le Maitre *et al.* 2002, but see Patel 2011). The costs associated with *Lantana* probably still exceed the benefits of its presence. However, incorporating the benefits that accrue to local communities may change the optimal distribution of removal effort across the landscape. Second, this lack of awareness of the potential positive economic value of IAS may lead to underestimation of the value of invaded ecosystems, which may bias spatial conservation planning.

Pimentel *et al.* (2001) estimate that 20-30% of IAS in the US, UK, Australia, India, South Africa and Brazil are considered pests and only a minority of these are likely to be serious pests (also see Lodge 1993). It is possible that

77 among the remaining species, an important portion may  
78 be socially and economically beneficial. Whether an IAS  
79 is beneficial depends on characteristics of the IAS, and of  
80 the ecosystems and social groups that are affected by it  
81 (García-Llorente *et al.* 2008). In Northern Ethiopia,  
82 invasive eucalyptus is used and sold as a building  
83 material and to construct farming tools; this species  
84 performs better in water- and nutrient-poor soils than  
85 indigenous species, and as a result is commonly grown in  
86 farmers' woodlots (Jagger & Pender 2003). However, in  
87 South Africa, eucalyptus is being removed from riparian  
88 areas to help restore natural water resources and  
89 increase the availability of potable water to communities  
90 (Marais & Wannenburgh 2008). It follows that the impact  
91 and role of IAS, and therefore control measures, are  
92 context specific. Part of this context relates to the  
93 socioeconomic factors that influence the relationships  
94 between IAS and communities.

95  
96 Similarly, the benefits of IAS vary within human  
97 communities as well as between them. The link between  
98 individuals' socioeconomic characteristics and their non-  
99 timber forest product harvesting behaviour has been well  
100 studied (e.g. Gavin & Anderson 2007; Lacuna-Richman  
101 2002; McSweeney 2002; Barham *et al.* 1999). For

102 instance, although it was once believed that those living  
103 in extreme poverty are particularly dependent on wild  
104 foods for subsistence (Scoones *et al.* 1992), the  
105 relationship is often more complex (e.g. Wilkie *et al.*  
106 2001). In some situations, wealthier households have  
107 greater capacity to hunt, consume and sell wild products  
108 (de Merode *et al.* 2004). The same complexities may also  
109 apply to the use of IAS, making the economic implications  
110 of removing an invasive species unclear. For example,  
111 communities bordering the Chitwan National Park in  
112 Nepal use a number of invasive species, including the  
113 plant *Mikania micrantha*. Rai *et al.* (2012) found that  
114 household socioeconomic characteristics influence *M.*  
115 *micratha*'s perceived value. Those families that were  
116 more dependent on forest products incurred more of both  
117 the costs and benefits associated with *M. micrantha* than  
118 less forest-dependent families. The value of ecosystem  
119 services often varies spatially and temporally; the  
120 management of invasive species that contribute to  
121 ecosystem services should therefore reflect this variability  
122 (Hershner & Havens 2008).

123

124 The relationship between biodiversity and ecosystem  
125 services is complex (Cameron 2002). However, higher  
126 biodiversity is generally positively correlated with higher

ecosystem service value in warm climates (Cardinale *et al.* 2012; Naeem *et al.* 2009; Costanza *et al.* 2007 Balvanera *et al.*, 2006). The effect of IAS species on biodiversity and habitat function is also complex (Hector and Bagchi, 2007; Schwartz *et al.*, 2000). Although the majority of the literature investigating the ecological impact of invasive species concludes that they are detrimental to native biodiversity, there are some examples where IAS assist native species, for instance through positive habitat modification (Rodriguez 2006). Similarly, the impact of IAS can change over time (Strayer *et al.* 2006). The invasive fire ant *Solenopsis invicta* in southern USA initially reduced the populations of other insects when first introduced in the 1980's. However, 12 years later *S. invicta* populations substantially declined and native arthropod species recovered to pre-invasion levels (Orrison & Loyd 2002). In this case, total arthropod biodiversity appears to have increased without compromising the population sizes of native species over the long term. It is plausible to suggest that in some instances, perhaps where there are empty niches (e.g., on some islands), the addition of IAS may increase biodiversity, ecosystem function & resilience and the value of ecosystem services (Young 2012; Young 2010; Hershner & Havens 2008). The



152 absolute socioeconomic costs and benefits of invasive  
153 species are hard to estimate because of the complex  
154 impact that they have on invaded ecosystems and  
155 species. However, arguably, this applies equally to the  
156 valuation of native species within wider ecosystems.

157

158 In order to explore these issues, we studied the economic  
159 benefits of the invasive Australian Red Claw crayfish,  
160 *Cherax quadricarinatus* (von Martens), within fishing  
161 communities of the Black River Lower Morass (BRLM) of  
162 southwest Jamaica (Figure 1). This study aims to answer  
163 three questions: a) can this invasive alien species provide  
164 an economically significant source of gross revenue, b)  
165 how are the economic benefits distributed over time and  
166 c) who within these communities benefits the most?

167

168 Increased household revenue is expected to contribute to  
169 increased consumption. Additional earnings may be  
170 particularly important for those that subsist on relatively  
171 low incomes, who are anticipated to have greater  
172 marginal utility from income (Ellis 1994). The temporal  
173 distribution of household liquidity is also important,  
174 especially in the absence of precautionary saving or  
175 functioning credit markets. Temporary or seasonal  
176 fluctuations in income may lead to corresponding

177 changes in consumption. This may lead to periods of  
178 cyclical poverty (Dercon and Krishnan 2000). Finally  
179 other socioeconomic characteristics may influence the  
180 capacity for individuals to mobilize resources or otherwise  
181 influence harvesting behaviour. Identifying the distribution  
182 of economic benefits across different groups is also  
183 useful for contextualising the benefit of additional  
184 revenue. For example, those with no alternative  
185 occupations would have a higher opportunity cost from  
186 not engaging in harvesting, than those that do. As a  
187 result, they may be the most dependent on the income  
188 derived from harvesting activity.

189

190 The study does not determine if there is a net economic  
191 benefit associated with the invasive crayfish to the  
192 communities within the BRLM. Instead it seeks to  
193 encourage landscape managers to consider possible  
194 economic benefits, as well as costs, within invaded  
195 ecosystems and compared to more pristine ecosystems.  
196 Accounting for the possible benefits, as well as costs,  
197 may improve conservation resource allocation within  
198 landscape management and improve the accuracy of  
199 ecosystem valuation.

200

## 201     **1.1 Study site**

202     The Black River Lower Morass is situated within the  
203     parish of St. Elizabeth. The parish is described by  
204     Campbell, Barker and McGregor (2011) as the  
205     ‘breadbasket of Jamaica’, owing to its importance as a  
206     domestic source of agricultural produce. The agricultural  
207     sector is dominated by small-scale farmers, which are  
208     deemed to be relatively prosperous relative to national  
209     living standards (McGregor, Barker and Campbell 2009).  
210     Fishing, using traditional gear, is a common occupation in  
211     the BRLM Ramsar site. Although a few individuals  
212     specifically target either native shrimp (*Macrobrachium*  
213     *spp.*) or invasive crayfish (*C. quadricarinatus*) with  
214     specialist gear, the vast majority catch both using the  
215     same harvesting equipment: homemade shrimp pots.  
216     Fishing is one of the most common occupations in the  
217     four target communities of the BRLM who operate from  
218     two landing stages in Community 1 and Community 2  
219     (Figure 1). Village names, and details that could be used  
220     to identify those villages, were kept anonymous because  
221     of the sensitive nature of some activities, including  
222     Marijuana cultivation. Fishermen from another village,  
223     further south in the BRLM, often use wire mesh traps that  
224     specifically target the invasive crayfish as opposed to  
225     traditional shrimp pots for native shrimp, and were not

226 included in the study. All caught shrimp and crayfish are  
227 sold to local women who then cook and sell them along  
228 roadsides throughout the country. The fishery requires  
229 relatively low capital inputs and has few barriers to entry.  
230 Of these barriers the most significant appear to be the  
231 purchasing of fish pots at c. USD\$1.20 per pot, for those  
232 unable to construct their own, and the construction and  
233 maintenance or borrowing of dugout canoes.

234  
235 Low flow and drought events, such as those found during  
236 the dry season within the BRLM (Figure 1), reduce  
237 hydrological connectivity and pool volumes. They also  
238 lower water quality (reduced dissolved O<sub>2</sub> as the result of  
239 decomposing organic matter) and increase salinity, all of  
240 which negatively impact *Macrobrachium spp.* abundance  
241 (Covich & Crowl 2006; Jayachandran 2001; Bowles *et al.*  
242 2000).

243  
244 The invasive crayfish (*C. quadricarinatus*) are native to  
245 rivers and streams of north Australia and Papua New  
246 Guinea (Carpentaria 2008) - areas that experience  
247 seasonal drought (Riek 1969). They have diverse feeding  
248 habits that vary between habitats (Jones 1989), are  
249 physically robust (Ruscoe 2002), tolerant of anoxic  
250 environments, and a wide range of salinities and

251 temperatures (Meade & Watts 2002; Meade *et al.* 1994).  
252 It is these characteristics, combined with their large size  
253 and edibility that make them ideal candidates for  
254 aquaculture. It also makes them successful invasive  
255 species, and they have established feral populations in  
256 Singapore, South Africa, Israel, Mexico, Jamaica and  
257 Puerto Rico (often escaping from aquaculture, Ahyong &  
258 Yeo 2007).



260  
261 Figure 1. The Black River Lower Morass (thick line) in the  
262 Saint Elizabeth Parish, in southwest Jamaica.

## 264 2. Methods

265 Two main methods of data collection were used:  
266 recording catches at landing stages and one-off semi-  
267 structured interviews. Additionally, informal observations  
268 and interviews were also conducted throughout the study  
269 period. Catch data included the weights of native shrimp  
270 and invasive crayfish and the number of pots hauled per

271 fisherman per day. Semi-structured interviews collected a  
272 range of variables that were used to model predictors of  
273 harvesting behaviour (Table 1).

## 274 **2.1. Catch data collection**

275 The target population was all shrimp fishermen  
276 (estimated c. 95) from the four target communities who  
277 use the landing stages in Community 1 and Community  
278 2. Because of the low absolute number of fishermen, we  
279 aimed to collect a complete census of all fishermen's  
280 harvesting activities. There are no accurate records of the  
281 number of fishermen within the four communities.  
282 However, evidence of shrimp harvesting was only found  
283 in areas accessible from the two landing stages. Forest  
284 and swamp patches adjacent to other accessible areas  
285 were not found to contain shrimp harvesting gear. The  
286 fishermen targeted within the study were the main  
287 resources users within the morass and of the invasive  
288 crayfish. Seventy-six out of an estimated ninety-five  
289 fishermen agreed to participate (54 and 22 from  
290 communities 1 and 2 respectively).

291

292 A sampling framework, in which catch data were  
293 collected on alternate days from each landing stage for  
294 six days, followed by two days of no catch data collection,  
295 was implemented. Catch data were collected between

296 07:30h and 14:30h when the majority of fishermen  
297 returned to landing stages. The catches were separated  
298 into native shrimp and crayfish (one species,  
299 *Macrobrachium rosenbergii*, was not included in the  
300 analyses because it was harvested using different fishing  
301 gear), then weighed using an electronic hanging scale  
302 (ElectroSamson™ Digital Hanging Scales, 25 kg ± 0.02  
303 kg). The number of pots hauled that day was also  
304 recorded. We conducted a pilot study in September 2010.  
305 Changes were made to the protocol and so pilot data was  
306 not included in the study. Data were collected between  
307 October 2010 and August 2011. A local fisherman was  
308 hired as a research assistant to help collect catch data,  
309 assist in conducting semi-structured interviews and act as  
310 a key informant and guide to the community. The  
311 research assistant had worked as a fisherman his entire  
312 life, as well as serving as an assistant on other research  
313 projects, and was well respected within the communities.  
314 The research assistant also provided information about  
315 the standard (universal across all fishermen-buyer  
316 transactions) seasonal price change between the wet and  
317 dry seasons, which was confirmed by other community  
318 members during frequent, informal discussions  
319 throughout the study period. Informal discussions with  
320 other community members were routinely used to

321 triangulate qualitative data provided by the research  
322 assistant and across participants.

323

## 324 **2.2. Semi-structured interviews**

325 During March 2011, 50 interviewees were randomly  
326 selected (using a random number generator in R (R  
327 Development Core Team 2005)) from the 76 participating  
328 fishermen from whom we collected catch data; 36 from  
329 the landing stage in Community 1 and 14 from the  
330 landing stage in Community 2. Semi structured interviews  
331 were conducted primarily at the landing stages or in  
332 private residences. Interviews were often conducted  
333 during wider informal discussions. An interview guide  
334 (see Supplementary Material 3) was used to ensure that  
335 all questions were answered during the interview whilst  
336 allowing the delivery of the questions to remain flexible.  
337 This was necessary to both aid comprehension, and  
338 because of participant's hesitancy to answer questions  
339 that they perceive could be used to identify them as  
340 cultivating marijuana or for taxation purposes. To this  
341 effect, no audio recording equipment was used. Instead  
342 data were recorded in a notebook. This data were  
343 subsequently coded and the relevant quantitative data  
344 were extracted.

345



346 We asked respondents which community landing stage  
347 they used, the number of family members who were  
348 dependent on them and their total fishing experience in  
349 years (or fractions of years). We also asked if participants  
350 had other sources of income and to indicate their  
351 perceived standards of living according to a self-ranked  
352 wealth scale. This self-ranked wealth scale asked  
353 participants to rank their financial security relative to their  
354 community. Although this did not provide absolute data  
355 on individuals' wealth, it did provide an indicator of  
356 participants' perceived relative wealth, which appeared to  
357 be an important determinant of harvesting behaviour.  
358 Although using self-ranked measures of wealth can be  
359 problematic, Bodegom *et al.* (2009) found a significant  
360 correlation ( $p > 0.001$ ) between the in-depth Demographic  
361 Health Survey (DHS) wealth index and self-reported  
362 wealth measures. Similarly, self-ranked measures of  
363 wealth have been successfully used by others including  
364 Williams *et al.* (2012).

365

366 Opportunistic informal questioning of fishermen during  
367 the whole study provided valuable qualitative data  
368 regarding behaviour and incentives under varying catch  
369 conditions. This contextual data was vital for developing a  
370 set of candidate models as detailed below (section 2.3). It

371 also allowed the validity of inferences observed in the  
372 data to be evaluated and questioned based on a  
373 qualitative understanding of the community and fishing  
374 system. No information that could identify individuals was  
375 retained because of the sensitivity of some of the  
376 fishermen's illegal activities.

### 377 **2.3. Analysis**

378 Data were converted from JA\$ to US\$ (JA\$84.7= US\$1  
379 (XE Currency Converter 2010)) and imperial to metric  
380 weights where appropriate. Using the catch data, we  
381 calculated the gross revenues from crayfish and native  
382 shrimp harvesting by fishermen and investigated the  
383 seasonality of catches (weight per fishermen day) and  
384 catch value (total value per fishermen day). To do this we  
385 used the Köppen climate classification system to  
386 determine dry months (following Peel, Finlayson &  
387 McMahon 2007). For tropical wet/dry forests and  
388 savannah, the pronounced dry season contains months  
389 with precipitation of less than 60 mm or less than  $(100 -$   
390  $[\text{total annual precipitation (mm)}/25])$ . Total rainfall over  
391 the study period was 1072 mm; therefore the 60 mm  
392 value was higher than the 57 mm value (calculated using  
393 the stated formula) used to determine dry months. As  
394 such, months with  $< 60$  mm rainfall (total for the month)  
395 were considered dry months. Each month was

396 designated as a dry or a wet month, depending on the  
397 total rainfall calculated for each month (using data from  
398 the Meteorological Service of Jamaica). The designated  
399 wet and dry months were used as different levels (wet vs.  
400 dry) of a factor (season) and the individual times when  
401 the fishermen were interviewed were used as replicates  
402 for each month. We used a generalised linear mixed  
403 model (GLMM; with the communities as the random  
404 factor) with a gamma distribution and reciprocal link  
405 function (if the data did not include a zero value) to  
406 assess the effects of the seasons on the average yield of  
407 native shrimp, and invasive crayfish, the average number  
408 of pots hauled, and the average value of the native  
409 shrimp and invasive crayfish and the value of the  
410 combined yields. If the data included a zero value, we  
411 used a normal distribution with a reciprocal or a log link  
412 function (depending on an assessment of the residuals).  
413 We then used a one-way ANOVA to assess the  
414 differences between seasons for each site, the  
415 differences between each site, and the differences  
416 between each site for a particular season for average  
417 yield, pots hauled and value (total and average).  
418 Following an assessment of the residuals, we found that  
419 the assumptions of this analysis were not upheld.  
420 Therefore yield and value data were first transformed

421 using  $\log_{10}(x + 1)$  before analysis. Average number of  
422 pots hauled data was not transformed because an  
423 assessment of the residuals indicated that the  
424 assumptions of the ANOVA were not violated. These  
425 statistical tests were performed using the GenStat  
426 Discovery Edition 4.0 (VSN International, Hemel  
427 Hempstead, UK) statistical package.

428

429 All subsequent data analyses were conducted using the  
430 statistics programme 'R' version 2.14.2 (R Development  
431 Core Team 2005). All socioeconomic variables were  
432 tested against each other for correlation using  
433 Spearman's rank correlation, one-way ANOVA, Kruskal-  
434 Wallis rank sum test and Pearson's Chi-squared tests in  
435 R.

436

437 Next, we created two measures of dependence on fishing  
438 to determine which types of fishermen might be  
439 benefitting most from presence of the crayfish. Generally,  
440 it is challenging to measure dependence on resources  
441 directly, since this requires information on (hypothetical)  
442 alternatives to harvesting were the resources not to exist.  
443 In many developing countries, shadow wage rates are  
444 hard to estimate as labour markets are thinly developed  
445 and may not always be cash based. Using gross revenue

446 as an indicator of harvester's *dependence* on native  
447 shrimp and invasive crayfish could be misleading, instead  
448 reflecting their individual capacity to mobilise resources or  
449 their effectiveness as fishermen. The distinction between  
450 the sizes of the gross revenue derived from harvesting  
451 activities, and the degree that individuals are dependent  
452 on that source of income, is due to several factors  
453 including the availability of alternative occupations and  
454 the opportunity cost of forgoing that revenue.

455

456 We therefore used two proxies for dependence. Firstly, i)  
457 mean daily harvest effort (mean number of pots hauled  
458 per fisherman per day across all days of data collection).  
459 Secondly, ii) intra-annual variation in harvesting effort (the  
460 change in harvest effort between the wet and dry season,  
461 for each fisherman).

462

463 We assumed that those harvesters who have the lowest  
464 mean harvest effort and who varied their harvesting effort  
465 the most in response to seasonal fluctuations in catches  
466 were less dependent on the resource than those who  
467 invest more effort into harvesting or maintain more  
468 consistent effort throughout the year, even when catches  
469 decline. We therefore investigated how socioeconomic  
470 variables (elicited during the semi-structured interviews)

471 influenced i) daily mean harvesting effort and ii) intra-  
 472 annual variation in harvesting effort. Equation (1)  
 473 describes the means by which we calculated intra-annual  
 474 variation in harvest effort ( $V$ ) for each fisherman.  $P$  is the  
 475 total recorded pots hauled per fisherman and  $D$  the total  
 476 number of possible harvesting days, respectively, during  
 477 the wet ( $w$ ) and dry ( $d$ ) seasons. Since monitoring effort  
 478 was consistent across both seasons, this provides a  
 479 combined indicator of changes in number of pots hauled  
 480 per day and changes in the number of days fishermen  
 481 are active in the fishery.

$$482 \quad V = 100 * [(Pd / Dd) - (Pw/Dw)] / (Pw/Dw) \quad (1)$$

484  
 485 Within the two analyses, we used Generalised Linear  
 486 Models (GLMs) to explore which socioeconomic  
 487 characteristics predicted daily mean harvest effort and  
 488 intra-annual variation in effort, with a Gaussian  
 489 distribution and identity link function. The choice of  
 490 explanatory variables was based on relevant literature,  
 491 semi-structured interviews with fishermen and  
 492 observations in the field (see Table 1 for a description of  
 493 variables). Because eight explanatory variables were  
 494 identified *a priori*, we fitted the global model and all  
 495 possible combinations of variables. We then used an

496 information-theoretic approach to avoid over-fitting,  
497 ranking our candidate sets of models using the corrected  
498 AIC (AICc) because of the small sample size (Akaike  
499 1974). In both candidate sets there was no model with a  
500  $\Delta AICc > 2$  and so we averaged across all models  
501 following Anderson & Burnham (2002). For each analysis,  
502 the 10 models with the lowest AICc and the averaged  
503 models are detailed in the Supplementary Material 1.  
504 There was a strong positive relationship between years of  
505 experience and the capacity of fishermen to make their  
506 own pots ( $F_{(43,1)} = 6.65$ ,  $p = 0.013$ ). Therefore, to avoid  
507 model redundancy, the pots variable was removed from  
508 the candidate set of both GLMs. The decision to drop this  
509 variable followed the reasoning that it was more likely that  
510 experienced fishermen would learn how to make pots  
511 than it was that those fishermen who know how to make  
512 pots would gain greater experience as a result.

Variable name	Variable type	Coding	Description	References	Overall		Community 1		Community 2	
					Mean	Std. error	Mean	Std. error	Mean	Std. error
community	binary	Community 1= 0 Community 2= 1	The landing stage that the fisherman operates from, which influences characteristics such as distance from markets.							
dependents	discrete		The number of dependents (spouses and children who are financially supported within the household) can either increase the constraints on, or availability of, labour.	(Mazera et al. 2007; McSweeney 2002; Barham et al. 1999)	3.55	0.37	4.39	0.75	3.14	0.62
experience	continuous		The number of years as a shrimp fisherman is an indicator of professional status and harvesting skill.	(Lacuna-Richman 2002)	28.00	2.59	30.69	2.92	22.07	5.08
occupation	binary	No alternative occupation= 0 Has one or more alternative occupations = 1	Fishermen with alternative occupations can re-distribute their effort in response to declining catches, thereby maximising incomes in ways that those who are solely reliant on shrimp harvesting cannot.	(Martin et al. 2013; Cinner et al. 2011; Ellis & Allison 2004; Mazera et al. 2007; Batterbury 2001; Ellis 2000)	0.93	0.03	0.97	0.03	0.86	0.10
wealth	ordinal	'I am living comfortably'= 4 'I am coping'=3 'I am living with some difficulty'=2 'I am living with extreme difficulty'=1	This scale is used as a rough proxy for wealth, whose impact on fishing behaviour, particularly when catches change, can be both positive or negative depending on other economic factors. Measuring wealth is challenging. We felt that a subjective measure of perceived standards of living was an adequate proxy for wealth in this study.	(Williams et al. 2012; Daw et al. 2012; Cinner et al. 2009; Takasaki et al. 2001; Cinner et al. 2011)	3.26	0.12	3.35	0.14	3.07	0.27
pots (not included)	binary	Yes=1, No=0	Do individuals use pots that they have constructed, as opposed to ones that have been purchased?		0.66	0.07	0.71	0.08	0.57	0.14
marijuana	binary	Yes=1, No=0	Do individuals cultivate marijuana alongside harvesting shrimp (which may be an alibi for being in the swamp)?		0.53	0.07	0.71	0.08	0.14	0.10
mean effort	scalar		Mean effort, as measured by the mean number of pots hauled per fisherman per day of data collection across the study period.		100.96	7.54	103.21	9.15	96.01	13.74
intra-annual variation in effort	continuous		A measure of an individual fisherman's change in harvest effort between the wet and dry season (%), defined according to fishermen's classification of the wet and dry seasons, to reflect traditional delineations.		11.3	14.7	12.0	19.7	9.8	18.6



### 514 **3. Results**

515 All fishermen within the target group were male. In each  
516 community 37.5% of catch days were recorded during the  
517 11-month period. We weighed 4,909 catches during this  
518 period. We attribute the disparity between participation  
519 rates between the two communities (all 54 in Community  
520 1 and 22 of 41 in Community 2) to greater suspicion  
521 towards the objectives of the project in Community 2,  
522 even though anonymity was assured and identities were  
523 unspecified during publication (individuals were identified  
524 using initials to allow data collection). Because of the  
525 lower participation rates in Community 2 there may be  
526 bias in our results, if the reasons for not participating are  
527 linked to fishing activities. Of the 50 participants selected  
528 for interview, 5 were unwilling to participate or did not  
529 provide sufficiently detailed responses. We therefore  
530 completed interviews with 31 individuals from Community  
531 1, and 14 individuals from Community 2.

532

#### 533 **3.1. The monetary value of the invasive crayfish** 534 **harvest**

535 The mean market value of individual fishermen's daily  
536 catch over the 11 months (incorporating seasonal price  
537 changes) was US\$22.81 with the invasive crayfish

538 making up US\$3.53 of that value. Informal discussions  
539 with fishermen indicate that the invasive crayfish is  
540 considered to be a by-catch of shrimp harvesting, as  
541 opposed to fishermen specifically targeting the invasive  
542 species. Additionally, other fishermen also catch the  
543 invasive species as by-catch using other fishing gear.  
544 Smaller invasive crayfish may not have been separated  
545 from the native shrimp catches. These results suggest  
546 that the total invasive crayfish catch values were probably  
547 lower than observed. From these figures, an approximate  
548 and illustrative gross annual revenue can be estimated;  
549 an 'average' fisherman, working the mean number of 5.95  
550 days per week, hauling the mean value of 104.82 pots  
551 per day, would earn gross revenue of approximately  
552 US\$7,077 per year. However, among individuals there is  
553 high variability in catch value, effort and gross value per  
554 unit effort. Effort varies from as little as 30 pots hauled  
555 per day to as many as 200 (including seasonal  
556 fluctuations in effort) and the maximum mean gross value  
557 per pot (across all pots hauled by one fishermen on one  
558 harvesting excursion) is nearly 520% greater than the  
559 minimum. Using the Köppen climate classification system  
560 analysis we determined that there were, in total, four dry  
561 months and seven wet months. Informal discussions with  
562 fishermen indicate that fishermen typically set more pots

563 during the wet season. However, anecdotal evidence  
564 suggests the study period covered an unusually dry  
565 November, when fishermen normally set a high number  
566 of pots; it was subsequently classified as a dry season  
567 month, when it would typically be considered to be in the  
568 wet season. This may have skewed our results  
569 concerning the number of pots hauled. Consequently, we  
570 found that the average number of pots hauled across all  
571 fishermen was significantly higher in the dry season (dry  
572 = 111 ( $\pm$  1.22 s.e.) vs. wet = 100.9 ( $\pm$  1.75 s.e.) pots day<sup>-1</sup>;  
573  $F_{(1,246)} = 24.53$ ,  $p < 0.001$ ).

574

575 Market prices and catch sizes both varied between the  
576 wet and dry seasons. Native shrimp and invasive crayfish  
577 prices rose during the dry season, from US\$6.44 to  
578 US\$7.73 and US\$3.86 to US\$5.15 per kilogram  
579 respectively. We found that the native shrimp yield was  
580 significantly higher in the wet than the dry months (dry =  
581 2.67 ( $\pm$  0.07 s.e.) vs wet = 2.95 ( $\pm$  0.09 s.e.) kg/ day<sup>-1</sup>;  
582  $F_{(1,246)} = 6.8$ ,  $p = 0.01$ ), when looking at all fishermen  
583 across the two communities, despite the lower effort,  
584 whilst the opposite was true for the invasive crayfish (dry  
585 = 1.11 ( $\pm$  0.04 s.e.) vs. wet = 0.56 ( $\pm$  0.05 s.e.) kg/ day<sup>-1</sup>;  
586  $F_{(1,246)} = 49.22$ ,  $p < 0.001$ ).

587

588 Across all fishermen, the gross revenue from the invasive  
589 crayfish was significantly higher during the dry months  
590 than the wet (dry = \$5.47 ( $\pm$  0.2 s.e.) vs. wet = \$2.29 ( $\pm$   
591 0.23 s.e.) US\$ day<sup>-1</sup>;  $F_{(1,246)} = 54.85$ ,  $p < 0.001$ ). The  
592 gross revenue of the native shrimp did not change over  
593 the seasons (dry = \$19.74 ( $\pm$  0.56 s.e.) vs. wet = \$18.99  
594 ( $\pm$  0.85 s.e.) US\$ day<sup>-1</sup>;  $F_{(1,246)} = 1.13$ ,  $p = 0.289$ ). The  
595 combined gross revenue of both the native shrimp and  
596 the invasive crayfish was higher during the dry season  
597 (dry = \$29.09 ( $\pm$  0.07 s.e.) vs. wet = \$24.63 ( $\pm$  0.07 s.e.)  
598 US\$ day<sup>-1</sup>;  $F_{(1,246)} = 25.97$ ,  $p < 0.001$ ). However, we did  
599 not find any statistically significant differences in catches  
600 or number of pots hauled between the two communities.

601

602 During March (the height of the dry season), the invasive  
603 crayfish accounts for, on average, approximately one  
604 quarter to one third of the total catch value. Harvesting  
605 invasive crayfish appears to reduce the variability in  
606 fishermen's incomes during the year.

607

608 Catch weight, pots hauled and catch value for each  
609 community mirrored the overall trends between seasons.  
610 Exceptions to this were the absence of statistical  
611 significance in the average number of pots hauled and  
612 the average yield of native shrimp, between seasons, in

Community 1. Supplementary Material 2 describe the results from the one-way ANOVA used to assess seasonal effects on catches, number of pots hauled and catch value between the two communities across the seasons, and their means and standard errors.

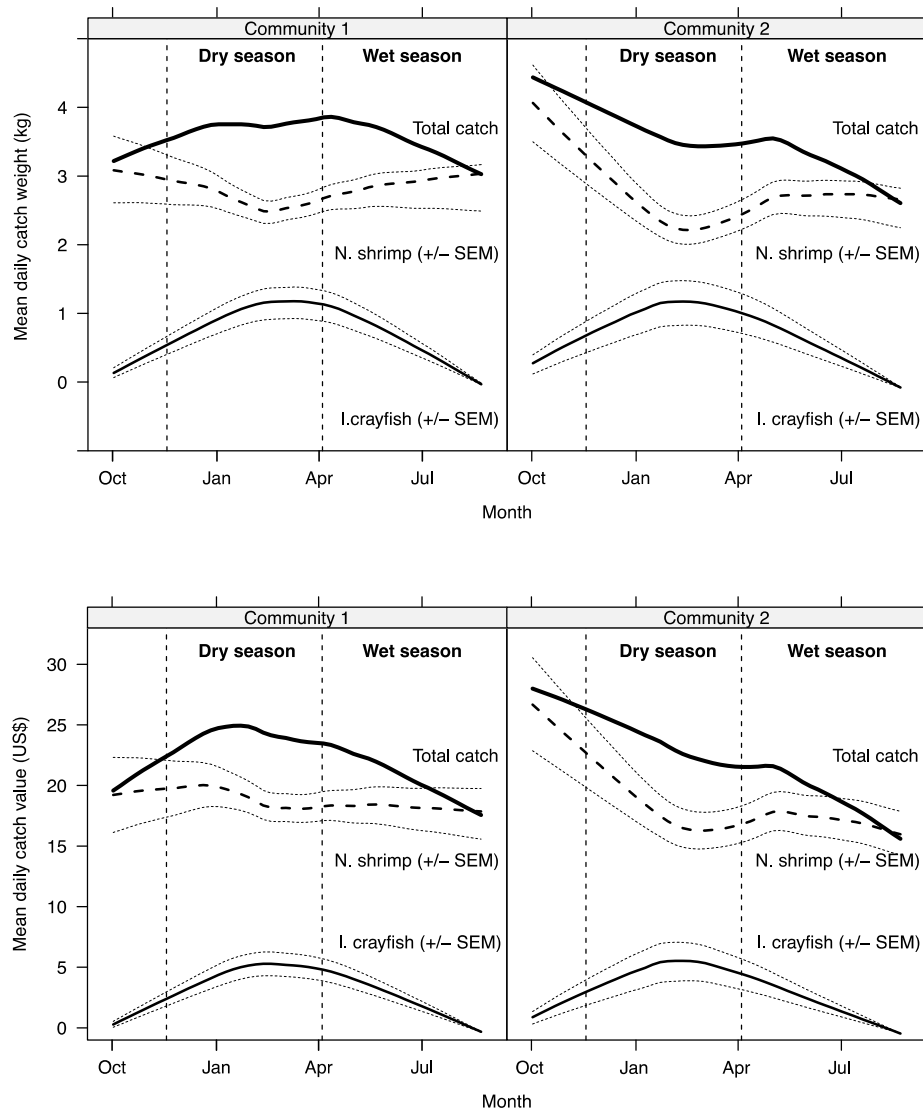


Figure 2. Smoothed seasonal trends in mean catch weight (top row) and mean catch value (bottom row) per trip for native shrimp (N. shrimp, dashed), invasive crayfish (I. crayfish, thin line) and total values (thick line) for the two communities including standard errors (+/-

SEM, thin dashed). Dry season is shown by vertical dashed lines.

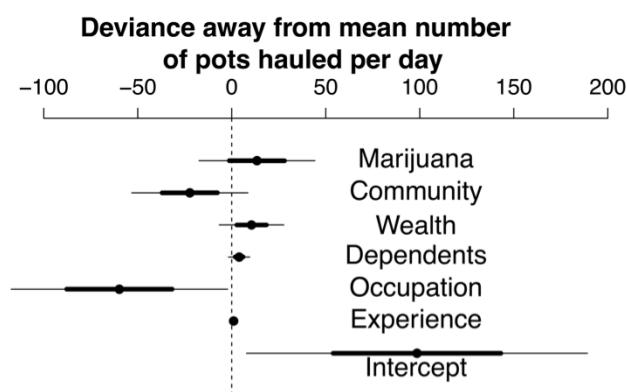
During semi-structured interviews and informal interviews, fishermen unanimously reported that they had observed a decline in native shrimp catches during their lifetimes. They suggested that the primary drivers of this decline were reduced water quality and an increase in the number of fishermen; none mentioned the invasive crayfish as a likely contributor. Although there is no empirical evidence to substantiate these claims, our key informant and research assistant also held these opinions.

### **3.2. Socioeconomic predictors of harvesting effort**

Marijuana cultivation was more common in Community 1 ( $\chi^2(1,44) = 10.27, p = 0.0013$ ), as was the likelihood of having an alternative occupation (aside from marijuana cultivation,  $\chi^2(1,44) = 4.25, p = 0.0391$ ). Those who cultivate marijuana are typically wealthier than those who do not ( $H(3) = 5.66, p = 0.12$ ).

Model averaging across all models in the candidate set (weighted by AICc, Burnham & Anderson 2002), we find that years of experience and having alternative occupations influence fishermen's mean harvest effort (Supplementary Material 1). It is estimated that on average those fishermen with alternative occupations set

653 nearly 60 fewer pots per monitored day, than those with  
 654 no alternative occupations (Figure 3). For each additional  
 655 year of fishing experience, fishermen set on average 1.1  
 656 more pots per day. Wealth, number of dependents and  
 657 marijuana cultivation all had positive effects on the  
 658 number of pots set, but these relationships were weak.  
 659 Those from Community 2 set around 22 fewer pots than  
 660 those from Community 1. However, the relationship is  
 661 only moderately strong, and according to the previous  
 662 analysis (discussed above) is not statistically significant.  
 663



664  
 665 Figure 3. Model-averaged coefficients for socio-economic  
 666 determinants of individual fishermen's mean daily harvest  
 667 effort, measured in number of pots hauled per day,  
 668 across all days of data collection during the study period.  
 669 The range shows the positive or negative impacts of the  
 670 characteristics on the mean number of pots hauled  
 671 across all fishermen. Points show the coefficient

estimates, thick lines indicate first confidence interval (68%) and thin lines indicate the second (95%).

### 3.3. Socioeconomic predictors of intra-annual variation in harvest effort

The second GLM found wealth to be an important determinant of intra-annual variation in harvest effort (the change in harvest effort for an individual fisherman between the wet and dry season) for some fishermen (Figure 4). Between those fishermen who have the highest and lowest wealth there is c.27 percentage points more variability between the wet and dry season; a fisherman who is 'living comfortably' (wealth category 4) reduces effort, on average, by 27 percentage points more than someone 'living with extreme difficulty' (wealth category 1). Having an alternative occupation was found to not have a clear effect on the variability between the wet and dry season.

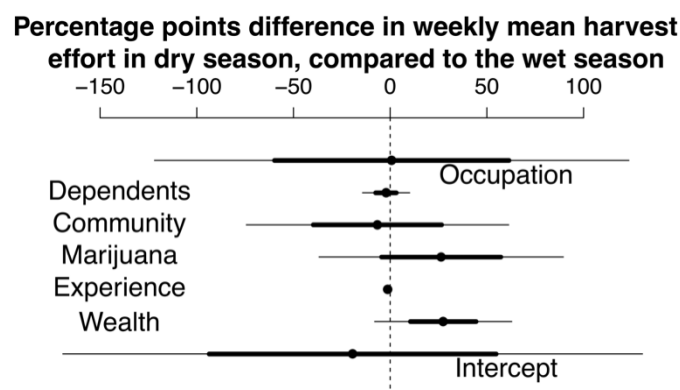




Figure 4. Model-averaged coefficients (in percentage points) for socio-economic determinants of intra-annual variation. 0 indicates no effect on seasonal changes in harvest effort, whereas an estimate of -10pp, for example, indicates that the factor is associated with an additional 10pp decline in harvest effort between the wet and dry season. Points show the coefficient estimates (as pp), thick lines indicate the first confidence interval (CI=68%), thin lines indicate the second (CI= 95%).

700

## 701 **4. Discussion**

### 702 **4.1. Can invasive alien species provide an** 703 **economically significant source of revenue?**

704 This study has quantified some of the gross economic  
705 benefits of the IAS, the Australian Red Claw crayfish. Our  
706 results suggest that the invasive crayfish provides an  
707 economically significant portion of fishermen's gross  
708 revenues, contributing approximately 15% of total catch  
709 value across all fishermen during the study period.  
710 However, this gross revenue does not occur evenly over  
711 time or between individuals. Revenue derived from  
712 harvesting invasive crayfish during the dry season  
713 reduces the seasonal variability in incomes (income  
714 smoothing). It was reported that the invasive crayfish's  
715 mobility over land (something *Macrobrachium spp.* are

716 incapable of) lead to their congregation in residual water  
717 bodies, making them easier to harvest. This may account  
718 for the observed increase in crayfish harvests during the  
719 dry season, as opposed to an absolute increase in their  
720 population size.

721

722 The temporal distribution of incomes has been  
723 recognised as an important factor in household  
724 economics. Seasonal household liquidity constraints  
725 suppress consumption and can lead to periods of cyclical  
726 poverty (Dercon and Krishnan 2000). Weak or non-  
727 existent credit markets, limited precautionary saving,  
728 seasonal variance in prices and other factors can further  
729 impede consumption smoothing (Baulch and Hoddinott  
730 2000; Chaudhuri and Paxson 2001; Rosenzweig 2001).  
731 According to Khandker (2009) 'when income smoothing  
732 does not happen, a failure to smooth consumption may  
733 result in food shortage and deprivation.'

734

735 Fishermen reported that during the dry season they had  
736 less income from shrimp harvesting (supported by our  
737 findings), and those that had alternative income  
738 generating activities would refocus their efforts on those  
739 activities. Our study did not explore the impact of  
740 seasonal fluctuations in income on consumption

741 behaviour. Yet, fishermen reported that the dry season  
742 was typically a more difficult period because of  
743 constrained liquidity.

744

745 Within this context harvesting of the invasive crayfish  
746 during the dry season probably leads to less volatile  
747 incomes over the year. This increases income availability  
748 during the dry season, which is typically a period where  
749 incomes are constrained, and therefore may have an  
750 important consumption smoothing effect. This  
751 consumption smoothing may be particularly important for  
752 the poorest fishermen who may face seasonal deprivation  
753 if they cannot access credit markets and have no  
754 precautionary savings. An additional benefit can also be  
755 speculated. The invasive crayfish are more resilient to  
756 environmental fluctuations in temperature, salinity, and  
757 water chemistry. In this respect, they may also be more  
758 resistant to human induced environmental shocks. They  
759 may be more persistent in the face of environmental  
760 degradation than native shrimp species, and  
761 subsequently may become an increasingly important  
762 component of fishermen's incomes.

763

764

765 This study did not seek to determine the impact of the  
766 invasive crayfish on the native shrimp population, and  
767 subsequently the incomes that might be derived from  
768 shrimp catches in the absence of the crayfish. Anecdotal  
769 evidence suggests that native shrimp catches had been  
770 declining since before the introduction of the invasive  
771 crayfish in Jamaica. The participating fishermen reported  
772 increasing numbers of fishermen and pollution as  
773 probable drivers of the decline. There have been few  
774 studies of the effects of *C. quadricarinatus* on invaded  
775 ecosystems, but invasive crayfish have caused significant  
776 global impacts, both ecologically and economically  
777 (Gherardi 2007). In the case of *M. micrantha* utilisation  
778 around the Chitwan National Park in Nepal, communities  
779 perceived the invasive shrub as an inferior forest product  
780 with associated economic costs as well as benefits (Rai  
781 *et al.* 2012). Rai *et al.* (2012) suggest “the farm  
782 household response to invasive plants is to make the  
783 best out of the worst situation”. This might describe the  
784 situation in BRLM, but it also seems possible that the  
785 crayfish is exploiting otherwise unoccupied niches on the  
786 island, increasing aquatic diversity. Higher native  
787 biodiversity has been found to increase stability of  
788 ecosystems (Cardinale *et al.* 2012).

789

## 790     **4.2. Who benefits most from the fishery?**

791     In small-scale fisheries, fishermen are often found or  
792     assumed to be the poorest within communities, and  
793     fishing is a more frequent occupation in poor communities  
794     (FAO 2012; Béné *et al.* 2007). Although there is no  
795     economic data from communities within the BRLM with  
796     which to compare fishing incomes, a wide degree of  
797     socioeconomic heterogeneity within the fishing  
798     communities was observed. Those who have no  
799     alternative occupations tend to have higher average  
800     harvest effort over the year. Individuals who have  
801     alternative and more profitable occupations can distribute  
802     their effort to maximise their income whilst managing risk.  
803     This is supported by current economic and social theory  
804     relating to subsistence livelihoods, where individuals  
805     diversify their livelihoods to achieve higher and more  
806     stable incomes (Martin *et al.* 2013; Ellis & Allison 2004;  
807     Batterbury 2001; Ellis 2000). Our results are consistent  
808     with Mazera *et al.* (2007) who found that greater non-  
809     fishing income, derived from alternative occupations, was  
810     associated with reduced fishing effort. Shackleton, Kirby  
811     & Gambiza (2011) explore the role of the invasive prickly  
812     pear (*Opuntia ficus-indica*) in incomes of poor trading  
813     households in South Africa. They highlight the conflict of  
814     interest between the South African Government, which is

815 concerned with the impact to the formal economy and  
816 environment, and the income and nutritional needs of  
817 local traders. They found that lower income traders were  
818 most benefited by the presence of the invasive prickly  
819 pear.

820

821 Individuals that are the most dependent on the fishery  
822 tend to be those with greater experience. It is these  
823 individuals who appear to benefit most from the presence  
824 of the invasive crayfish. Lacuna-Richman (2002)  
825 suggested that older members of communities in Leyte,  
826 in the Philippines, were more dependent on non-timber  
827 forest products because they had both fewer alternative  
828 livelihood options and greater harvesting skills than  
829 younger members. However, our study did not find a  
830 significant correlation between 'experience' and presence  
831 or absence of an alternative 'occupation', which indicates  
832 that older or more experienced fishermen did not  
833 necessarily have fewer livelihood options available to  
834 them.

835

#### 836 **4.3. Who benefits most from dry season** 837 **presence of crayfish?**

838 During the dry season, native shrimp catches decline and  
839 invasive crayfish catches increase. In this study, we are

840 assuming that those with the least intra-annual variation  
841 in harvest effort are choosing to maintain their harvesting  
842 levels because they are most dependent on it. Again, as  
843 a logical extension, they also derive the greatest benefit  
844 from the invasive crayfish, which stabilises catches during  
845 the dry season. Within the BRLM, those with low self-  
846 reported wealth reduce their harvesting effort less during  
847 the dry season relative to the wet, than do those who  
848 consider themselves to be wealthier.

849

850 Although Cinner *et al.* (2011) found that fishermen  
851 reported that they would increase their harvesting effort in  
852 response to a decline in catches, Hoorweg *et al.* (2006)  
853 observed that the wealthier fishermen on the Malindi-  
854 Kalifi coast of Kenya were more inclined to reduce fishing  
855 effort in response to a decline in catches. Similarly,  
856 Hoorweg *et al.* (2006) found that those who had a range  
857 of occupations generally had a more positive attitude  
858 towards conservation of declining catch populations. This  
859 suggests that the fishermen's response to changes in  
860 catches is influenced by other socioeconomic  
861 characteristics. Our study has found similar complexity in  
862 behavioural responses to changing seasonal catch levels  
863 within the community. Although there is an overall  
864 increase in mean harvest effort during the dry season,

865 anecdotal evidence suggests this was atypical.  
866 Additionally, despite statistical significance, it is unclear if  
867 the observed mean change (an additional c.10 pots per  
868 day) is socially and economically significant. As a result  
869 this limits the wider conclusions that can be drawn  
870 regarding behavioural responses to changes in catch  
871 conditions. Pollnac *et al.* (2001) found that there are a  
872 wide variety of income and non-income factors that affect  
873 fishermen's readiness to leave fisheries in Southeast  
874 Asia, including non-economic job satisfaction. Our study  
875 differs in that it looks at seasonal changes in effort as  
876 opposed to individuals permanently leaving a fishery.  
877 Nevertheless, factors such as job satisfaction may also  
878 play an important role in determining changes in seasonal  
879 effort, though this was not explored in the present study.

880  
881 Financial security is a reflection of other socioeconomic  
882 characteristics, such as employment history and number  
883 of dependents. The effects of wealth on wild product  
884 harvesting behaviour are complex (Takasaki *et al.* 2001).  
885 Some studies have found that less wealthy families  
886 harvest more wild products, or are more reliant on them  
887 (Shackleton *et al.* 2011). Others have found more  
888 complex relationships, tied to land tenure and other  
889 assets that allow individuals to invest resources that allow



890 them to increase returns on effort (Williams *et al.* 2012).  
891 Gavin & Anderson (2007) suggest that the effects of  
892 wealth on harvesting behaviour are confounded by other  
893 socioeconomic and environmental factors.

894

895 The relationship between poverty and small-scale  
896 fisheries in developing countries, once thought to be  
897 close, is now understood to be more complex (Béné  
898 2003). In some circumstances, where the opportunity  
899 cost of time is low, the supply of available labour can  
900 saturate open access fisheries, reducing incomes to the  
901 level of the opportunity cost or shadow wage rate (Béné  
902 2009). In short, incomes from small-scale or artisan  
903 fisheries may be set exogenously (a function of labour  
904 supply and alternative and more profitable occupations,  
905 which have higher barriers to entry), and are normally the  
906 least profitable activity within communities. Within the  
907 BRLM we have not determined if this is the case.  
908 However, those who are poorest are likely to remain in  
909 the fishery when catches decline because of a lack of  
910 capacity to adapt to changes in catch by mobilising  
911 resources which would allow them to engage in  
912 alternative occupations. In turn, this may allow them to  
913 attain higher incomes and subsequently have greater  
914 financial security (Badjeck *et al.* 2010). To the extent that

915 the invasive crayfish stabilises seasonal incomes and  
916 possibly consumption, it is the poor who appear to benefit  
917 most from its presence.

918

## 919 **5. Conclusion**

920 Although IAS continue to pose significant ecological and  
921 economic causes for concern, our evidence suggests that  
922 to help achieve a more optimal allocation of both  
923 development and conservation effort, unbiased  
924 accounting of their benefits as well as their costs is  
925 required. Schlaepfer *et al.* (2011) argue that the benefits  
926 of introduced and invasive species to ecosystems and  
927 ecosystem functions are underestimated. Such non-  
928 native species may fill ecological niches that become  
929 vacant as the result of other anthropogenic factors (or are  
930 vacant because of island effects), foster habitat  
931 restoration and support ecosystem functions. Introduced  
932 species can also provide novel non-timber forest  
933 products, bushmeat or other wild harvest products. We  
934 share Shackleton, *et al.*'s (2011) conclusion that there is  
935 a need for a more nuanced approach towards the  
936 management of IAS that balances both local livelihood  
937 needs and wider environmental and social concerns. The  
938 positive contributions of IAS need to be recognised and  
939 incorporated into environmental management efforts,

940 when considering the eradication of IAS and when  
941 calculating the value of invaded ecosystems.

942 **Acknowledgement**

943 TP thanks Mr M. and his family for welcoming him into their family and the  
944 authors thank all those fishermen who gave their time and set aside personal  
945 reservations to participate in the study. TP thanks Kurt Propser for his useful  
946 comments. The authors also thank the MacArthur Foundation (grant number  
947 96010-0) for their financial support during data collection.

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